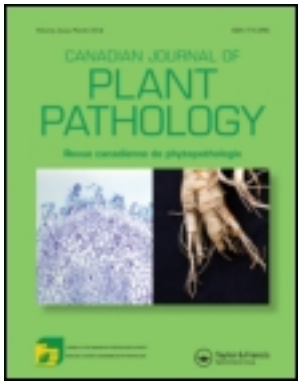

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Receptivity of barley to *Puccinia graminis* f. sp. *tritici*

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The receptivity of barley genotypes (*Hordeum vulgare*) was studied in seedlings and adult plants in the greenhouse and in adult plants in the field to races 113-RTQ and 151-QSH of *Puccinia graminis* f. sp. *tritici*. In the greenhouse, significant differences in number of uredia/cm^2 of leaf were detected due to the effects of races, host genotypes, and their interaction. The cultivar Hiproly was most receptive (had the most uredia) and 80-TT-29 was least receptive (had the fewest uredia) to both races at both growth stages. With race 151-QSH, genotypes with the T-gene, 80-TT-29 and Manker had low weighted infection types (seedling stage), moderately resistant host responses (adult stage), and lower receptivity (both growth stages) than cultivars lacking this gene. With race 113-RTQ, the T-gene was associated with low receptivity only in 80-TT-29. The data suggest that gene(s) other than the T-gene may confer receptivity to *P. graminis* f. sp. *tritici*. The ranking of genotypes and the relative differences in receptivity were similar in seedling and adult plants. In the field, genotypes with the T-gene had mostly moderately resistant reactions and fewer uredia than those without the gene. The significant race × host genotype interaction in this study suggests that receptivity in barley varies due to the specific host-parasite combination.
Additional key words: Disease resistance, wheat stem rust, infection frequency, *Hordeum vulgare*.

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On a étudié la réceptivité aux races 113-RTQ et 151-QSH de *Puccinia graminis* f. sp. *tritici* de différents génotypes d'orge (*Hordeum vulgare*) en serres sur des plantules et des plantes adultes et aux champs sur des plantes adultes. En serres, on a détecté des différences significatives dans le nombre d'urédies/cm^2 de feuille suivant les races, le génotype de la plante-hôte et leur interaction. Le cultivar Hiproly était le plus réceptif (avait le plus d'urédies) et la lignée 80-TT-29 était la moins réceptive (avait le moins d'urédies)) dans les deux stades de développement étudiés. Dans le cas de la race 151-QSH, les génotypes ayant le gène T, soient 80-TT-29 et Manker, présentaient un faible niveau d'infection au stade plantule, une réaction de résistance moyenne au stade adulte, et une réceptivité plus faible (dans les deux stades de développement) que celle démontrée par les cultivars dépourvus de ce gène. Dans le cas de la race 113-RTQ, le gène T n'est associé à une faible réceptivité que pour la lignée 80-TT-29. Ces résultats suggèrent qu'un ou des gènes autres que le gène T soient responsables de la réceptivité à *Puccinia graminis* f. sp. *tritici*. Le classement des génotypes et leur différence relative de réceptivité étaient semblables pour les plantules et les plantes adultes. Au champ, la plupart des génotypes avant le gène T étaient modérément résistants et présentaient moins d'urédies que ceux dépourvus du gène. L'interaction significative race-génotype de la plante-hôte suggère que la réceptivite de l'orge varie suivant une combinaison hôte-parasite qui est spécifique.
Mots-clés additionnels: résistance aux maladies, rouille de la tige du blé, fréquence d'infection. *Hordeum vulgare*.

Components of resistance that reduce the apparent infection rate during an epidemic have received considerable attention because they may be indicative of a more durable type of resistance than that differentiated by low infection types. One of the major components of this resistance is the number of uredia that form on plants after uniform inoculation (receptivity).

The T-gene conditions resistance in barley (*Hordeum vulgare* L.) against *Puccinia graminis* Pers. f. sp. *tritici*, and it has been effective since it was first introduced about 50 years ago (8,13). If more were known about the resistance conditioned by this gene, valuable information might be gained about durable resistance of cereals to rust fungi. The T-gene confers resistance recognized by infection types in barley (8), but it is not known to be involved in the resistance recognized by the slow development of rust. The purpose of this investigation was to evaluate receptivity in barley infected with *P. graminis* f. sp. *tritici* and to determine the possible effect of the T-gene on receptivity.

Materials and methods

Greenhouse tests with seedlings. Barley genotypes that lack the T-gene, Hiproly (C.I. 3947), Bonneville (C.I. 7248), and 80-tt-30 (C.I. 16130), and those that possess it, Manker (C.I. 15549) and 80-TT-29 (C.I. 16129), were studied because in preliminary tests they differed in resistance as measured by receptivity to races 113-RTQ and 151-QSH of *P. graminis* f. sp. *tritici*. Lines 80-TT-29 and 80-tt-30 are near-isogenic for the T-gene being derived from selections of the F_{29} generation of the crosses (Wisconsin Barbless × Chevron) × Composite Cross 11 (J.G. Moseman, personal communication).

Barley plants were grown in plastic pots filled with vermiculite in a greenhouse at about 20°C. When day length was less than 12 h/day, supplemental fluorescent light (11 000 lux) was

provided. Fertilizer (23-19-17, N-P-K) was applied at a rate of 0.3 g/pot after the plants had emerged. Prior to inoculation, excess plants were removed from the pots leaving four plants of similar size per pot. A completely randomized design was used. There were 6 replicates (pots) with 4 subsamples per replicate (plants) for each race × host genotype combination. Inoculum of races 113-RTQ and 151-QSH of *P. graminis* f. sp. *tritici* was increased, stored, and prepared for use following procedures described by Steffenson et al. (15). The purity of the pathogen races was checked using the procedures and differential cultivars of Roelfs and McVey (9). Races 113-RTQ and 151-QSH have been two of the most common or virulent races found on barley in the last 5 years (9).

Seedlings that were 7 days old were inoculated with a suspension of 1.23 ± 0.02 mg uredospores/8 mL light-weight mineral oil, using a quantitative inoculator (1). The inoculator delivered about 0.05 mL oil to the adaxial side of each leaf with the leaves set 12 cm from the nozzle of the inoculator. The inoculated portions of the leaves were marked with indelible ink to designate the area where uredia were to be counted.

After inoculation, the plants were placed in a dark dew chamber at 18° ± 1°C for about 15 h. Then the chamber was illuminated with fluorescent tubes (10 000 lux) for about 1 h before the door was opened so the plant surfaces could dry off. Next, the plants were removed from the dew chamber, fertilized (0.3 g/pot of 23-19-17, N-P-K), and placed in a growth chamber at 25°C, with a relative humidity of over 90%. Illumination (22 600 lux) was supplied by fluorescent and incandescent lamps for 13 h/day.

Two weeks after inoculation, infection types and numbers of uredia were recorded. All host genotypes tested gave mesothetic reactions to the pathogen races and so the response was expressed as a weighted infection type calculated from the kind and relative frequency of the infection types (IT) present (15). Only uredia were considered for receptivity evaluations because they possess spores and are important in the rate of epidemic development. Chlorotic and necrotic flecks were of little consequence in this study because they were seldom observed on any of the cultivars. Receptivity was expressed as the number of uredia/cm^2 of leaf surface, and the inoculated area of the leaf was measured with a portable leaf area meter (Lambda Instruments Corporation, Model LI-3000, Lincoln NE 68504).

Greenhouse tests with adult plants. Barley entries were sown in soil in plastic pots (3 seeds/10 cm diameter pot) and placed in a greenhouse at about 18°C where approximately 11 000 lux of supplemental fluorescent light was provided. Two weeks after planting, the plants were thinned to one per pot. A water soluble fertilizer (23-19-17, N-P-K, 1.4 g/pot) was applied 3 weeks after planting. One day before inoculation, secondary tillers were removed. Cultivar Bonneville was not included in the adult plant tests because of limitations of greenhouse space.

Plants at the early kernel-fill stage of growth were inoculated with race 113-RTQ or 151-QSH of *P. graminis* f. sp. *tritici*. A suspension of about 2.5 ± 0.05 mg uredospores/8 mL light-weight mineral oil was sprayed onto the stems of plants with the quantitative inoculator (1). Plants were set 12 cm from the inoculator, and about 0.08 mL of oil was delivered per stem. A randomized complete block design was used in this experiment; the eight race × host genotype treatment combinations constituted a single block. There were 12 blocks in the experiment.

After inoculation, the plants were placed in a dark dew chamber overnight at 20°C ± 2°C. At 0800 h, the dew chamber was illuminated with three metalarc bulbs; light intensity varied from 9700 to 12 900 lux on the inoculated portions of the culm. At 1030 h, the chamber door was opened to allow the plant surfaces to dry off slowly. Plants were taken from the dew chamber and fertilized again at a rate of 1.4 g/pot, using the formulation 23-19-17 of N-P-K. They were later placed in the greenhouse at about 18°C and illuminated with 11 000 lux of fluorescent light plus day light.

Three weeks after inoculation, the type and number of uredia on the flag leaf sheath were recorded; receptivity was expressed as the number of uredia/cm^2.

Field tests. Manker, Bonneville, Hiproly, 80-TT-29, and 80-tt-30 were evaluated for receptivity to races 113-RTQ and 151-QSH during the summer of 1982 at Rosemount, MN. Two separate plots, one per race, were planted 150 m apart in an attempt to limit the exchange of inoculum between plots. Entries in the plots were arranged in a randomized complete block design with six blocks per plot. The blocks were spaced 1.2 m apart and were surrounded with Era wheat (*Triticum aestivum* L., CI. 13986), a cultivar resistant to the prevalent races of *P. graminis* f. sp. *tritici*.

Plants were inoculated when the early maturing cultivars were in the early kernel-fill stage of growth. Uredospores, suspended in a light-weight mineral oil, were applied to the plants using a backpack mist-blower (10). A suspension of 0.24 mg uredospores/mL oil was applied at a rate of about 2.8 mL oil/m row. Conditions for natural

Table 1. Number of uredia/cm², range of infection types and weighted infection types on seedlings of barley genotypes uniformly inoculated with two races of *Puccinia graminis* f. sp. *tritici* in the greenhouse at 25°C

Entry	Possesses T-gene	Uredia/cm²[a]		Infection type range		Weighted infection type[b]	
		Race 113-RTQ	Race 151-QSH	Race 113-RTQ	Race 151-QSH	Race 113-RTQ	Race 151-QSH
Hiproly	-	9.3a	5.7b	1-4	1-4	1.8ab	1.5bc
Bonneville		2.7c	0.5d	1-3	1-3	2.2a	0.9de
80-tt-30		2.5c	2.4c	1-3	1-3	1.8ab	2.0ab
80-TT-29	+	1.8c	0.2d	1-2	1	1.2dce	0.4f
Manker	+	4.4b	0.3d	1-2	1	1.2dce	0.7fe

[a]Values are means of 24 plants. Means with different letters are significantly different at P = 0.05 according to Tukey's procedure.

[b]General equation: $\frac{\Sigma \text{ (Rank} \times \text{Infection Type Code)}}{\Sigma \text{ (Rank)}}$ = Weighted Infection Type. The most prevalent infection type is assigned the highest rank value and the least prevalent infection type the lowest rank value (15).

infection with stem rust were poor during the first part of the summer, so it is assumed that no infection due to exogenous sources had occurred prior to inoculation. This assumption was supported by the fact that susceptible wheat and rye indicator plants in the test plots were not infected during the course of the season. Rye cultivar Prolific (*Secale cereale* L., CI. 26) was used to detect the presence of *P. graminis* f. sp. *secalis* in the plots. The wheats W2691Sr10, W2691SrTt1, and Vernstein were used to monitor the presence of *P. graminis* f. sp. *tritici* in the plots because they react differentially with races 113-RTQ, 151-QSH, and 15-TNM. Race 15-TNM was monitored because it is the most common naturally occurring race in Minnesota. Additionally, racial identity tests were made on 20 collections from each plot and, only the races originally placed in the respective plots were present in those plots at the time data were collected.

Two weeks after inoculation, primary uredia were counted on 20 randomly selected culms/entry in each block before secondary spread of the pathogen was evident. Also, the host response was recorded on each entry. Receptivity was expressed as the number of uredia/culm. Since the data of all 3 receptivity experiments consisted of counts including zero and followed most closely the Poisson distribution, the Freeman-Tukey transformation (17) was applied to the data to correct for nonconstant variance and nonnormality. After analysis of variance, differences among treatment means were tested for significance using Tukey's procedure.

Results

Greenhouse tests with seedlings. Significant differences in uredia/cm² were observed due to the effects of the races, host genotypes, and their interaction. Race 113-RTQ produced significantly more uredia than race 151-QSH on all entries except 80-tt-30 (Table 1). The greatest number of uredia of both races formed on Hiproly and the least on 80-TT-29. The significant race × host genotype interaction appeared to be due primarily to the production of more uredia on 80-tt-30 with race 151-QSH than was expected based on the trend of the other entries. The T-gene in Manker and 80-TT-29 conferred resistant reactions, as these entries had the lowest weighted infection types to both races. Race 113-RTQ produced greater weighted infection types on all cultivars except 80-tt-30.

Greenhouse tests with adult plants. As in the seedling tests, significant differences in receptivity were observed in adult plants due to the effects of the races, host genotypes, and their interaction. Race 113-RTQ produced significantly more uredia than race 151-QSH on Hiproly and Manker, but not on 80-TT-29 and 80-tt-30 (Table 2). With both races, the greatest number of uredia formed on Hiproly, the least on 80-TT-29. Again, as in the seedling test, the race × host genotype interaction was significant due primarily to greater production of uredia by 151-QSH on 80-tt-30. All entries ranged from moderately susceptible to susceptible to both races with the exception of Manker and 80-TT-29 which displayed some moderately resistant host responses to race 151-QSH.

Field tests. The effects on receptivity due to host genotypes and the race × host genotype interaction were statistically significant. The race effect could not be tested statistically because the experimental design included only one replication for races. Race 113-RTQ produced more uredia/culm than 151-QSH on most entries, but this difference was significant only on Hiproly (Table 3). The receptivity of the genotypes varied greatly in the field: the greatest number of uredia formed on Hiproly and the least on Manker and 80-TT-29. The race × host genotype interaction appeared to be due primarily to a greater number of uredia

Table 2. Number of uredia/cm² and host response on flag leaf sheaths of adult barley genotypes uniformly inoculated with two races of *Puccinia graminis* f. sp. *tritici* in the greenhouse at about 18°C

Entry	Possesses T-gene	Uredia/cm²[a]		Host response[b]	
		Race 113-RTQ	Race 151-QSH	Race 113-RTQ	Race 151-QSH
Hiproly	-	2.3a	0.8bc	MS-S	MS-S
80-tt-30	-	0.3cd	0.3cd	MS-S	MS-S
80-TT-29	+	0.3cd	0.1d	MS-S	MR-MS
Manker	+	1.2b	0.1d	MS-S	MS-MR

[a]Values are means of 12 plants. Means with different letters are significantly different at P = 0.05 according to Tukey's procedure.

[b]S = large uredia (greater than 3 mm long) without chlorosis. MS = medium uredia (2 to 3 mm long) often associated with chlorosis. MR = small uredia (1 to 2 mm long) associated with much chlorosis.

forming on Bonneville with race 151-QSH than was expected based on the trend of the other entries. Genotypes with the T-gene gave mostly moderately resistant reactions to both races, whereas those lacking the gene gave mostly susceptible reactions.

Discussion

The receptivity of barley to *P. graminis* f. sp. *tritici*, as measured by the number of uredia forming on plants after uniform inoculation, has not been previously studied. Sellam and Wilcoxson (12) reported that some barley cultivars may differ in receptivity to *P. graminis* f. sp. *tritici*. Our data indicate that barley cultivars indeed vary in receptivity to *P. graminis* f. sp. *tritici*, whether tested as seedlings or as adult plants in the greenhouse and in the field. Differences among host genotypes in receptivity to cereal rust pathogens have been noted by other workers (4,5,6,7,10,14). Additionally, our data show that receptivity may vary due to the host-parasite interaction. This interaction, detected in each of the tests of this study, suggests that receptivity can be a race specific phenomenon as indicated by others (3,4,5).

In the *Zea mays-P. sorghi* (2), *Triticum aestivum-P. graminis* f. sp. *tritici* (4,11), and the *Solanum* spp.-*Phytophthora infestans* (16) host-parasite systems, low receptivity of cultivars has been considered to be a major component of resistance in controlling epidemics. The present work indicates that low receptivity may help protect some barley cultivars from stem rust, but this aspect should be investigated more thoroughly.

The presence of the T-gene in genotypes was not always associated with a low number of uredia/cm². In greenhouse tests with race 113-RTQ, Manker was more receptive than 80-TT-29 and 80-tt-30, and the near-isogenic lines (80-TT-29 and 80-tt-30) were equally receptive with race 113-RTQ. This suggests that gene(s) other than the T-gene may be involved in conferring receptivity to *P. graminis* f. sp. *tritici* in barley. With race 151-QSH, host genotypes that possess the T-gene had low receptivities at both growth stages. Bonneville had a relatively low receptivity to race 151-QSH in the seedling stage even though it does not carry the T-gene. We concluded that Bonneville may carry gene(s) for low receptivity to race 151-QSH. Additionally, low weighted infection types and resistant host responses appear to be correlated with low receptivity in seedlings and adult plants infected with race 151-QSH, but not with race 113-RTQ.

The receptivity characteristic in the barley entries was constant at the two growth stages tested in the greenhouse; the ranking of the genotypes and the relative differences in receptivity were similar in the seedling and adult plant tests made at 25° and 18°C, respectively.

Testing cultivars for differences in their ability to prevent the formation of uredia requires that plants be uniformly inoculated. This requirement was thoroughly tested when the Andres inoculation device was developed (1) and in tests preliminary to the experiments reported in this paper. In the preliminary tests both mineral oil and talc were evaluated as carriers of urediospores and no effect of the carrier was detected on the formation of uredial types or numbers. Mineral oil was used for our experiments because it is most compatible with the inoculation device.

In the field tests, the entries with the T-gene had mostly moderately resistant host reactions and were significantly less receptive than entries without the gene. Genotypes lacking the T-gene had susceptible host reactions. Among this group, Hiproly was significantly more receptive than Bonneville or 80-tt-30 to both races. This suggests that although the host reaction indicated susceptibility, Bonneville or 80-tt-30 possess a gene(s) that reduce receptivity to races 113-RTQ and 151-QSH. This same result could also be seen in both seedlings and adult plants in the greenhouse to race 113-RTQ.

Table 3. Number of uredia/culm and host response of barley genotypes uniformly inoculated with two races of *Puccinia graminis* f. sp. *tritici* in the field

Entry	Possesses T-gene	Uredia/culm[a] Race 113-RTQ	Uredia/culm[a] Race 151-QSH	Host response[b] Race 113-RTQ	Host response[b] Race 151-QSH
Hiproly	–	92.1a	48.3b	S	S
Bonneville	–	14.7c	15.3c	S	S
80-tt-30	–	10.2cd	7.0d	S-MS	S-MS
80-TT-29	+	1.3e	0.2e	MR-MS	MR
Manker	+	1.0e	0.3e	MR-MS	MR-MS

[a]Values are the means of six blocks with 20 samples/entry from each block. Means with different letters are significantly different at P = 0.05 according to Tukey's procedure.

Low receptivity was closely associated with the presence of the T-gene in host genotypes in the field; however, this trend was not always apparent in greenhouse trials. The reasons for this lack of agreement are not known, but differences in environmental conditions and inoculation procedures are probably involved. This demonstrates the need for verifying greenhouse data in the field.

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